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Stereopsis: Where Depth is Seen

Dispatch

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Disparity-selective cells appear to occur in all parts of the visual cortex, but a recent fMRI study finds that some cortical areas are more strongly associated with disparity than others. More sophisticated tests of binocular function may be needed to identify the properties of single neurons that support this specialization.

A fundamental organizing principle of the brain seems to be that anatomically discrete regions perform separate tasks. The extent of this specialization is clearest in the visual system, where the cerebral cortex is subdivided into distinct areas, each of which makes a different contribution to the processing of visual images [1]. These areas were originally identified on anatomical grounds (and simply identified with numbers V1, V2, V3…), then physiological investigations indicated that different subdivisions have different properties [2]. The clearest example of such specialisation is provided by V5 (also called MT) in the primate brain, which plays a crucial role in processing moving images (reviewed in [3]), but has little to do with the processing of shape or color.

One visual function which is not clearly identified with an anatomically distinct pathway is stereopsis — our ability to combine images from two eyes to perceive depth (Figure 1). If this aspect of visual processing is not localized in the way that motion processing is, then studies comparing stereo and motion may provide valuable insights into what principles dictate the need for anatomical localization of function. Such an endeavor depends critically on the view that there is no anatomical pathway specialized for stereopsis. While some recent physiological evidence adds support to this view [4–6], a recent imaging study in humans [7] indicates that there may after all be a degree of specialization for stereopsis in some brain areas.

In order to reconcile these recent observations, it is useful to consider further the distribution of visual operations between pathways. A distinction that has been used for many years divides visual cortical areas into two groups: a ‘dorsal stream’, which is largely concerned with object location and movement, and a ‘ventral stream’, largely concerned with object shape and color [8]. It has been argued that stereopsis is a function of the dorsal stream, but this idea was largely derived from psychophysical experiments [9]. These provide (at best) only indirect evidence about the anatomical location of visual function. One physiological observation used to suggest a role for the dorsal stream in stereopsis was that the cortical areas of the dorsal stream all contained disparity-selective neurons. However, there was not a well-documented lack of disparity-selective neurons in the ventral stream. Rather, several areas within the ventral stream had not been examined for disparity-selectivity. Three recent studies have addressed this imbalance, and found disparity selectivity in cortical areas V4 [4,5] and TE [6], central components of the ventral stream. Another recent study [10] found disparity selectivity in area V3, part of the dorsal stream with connections to ventral stream areas.

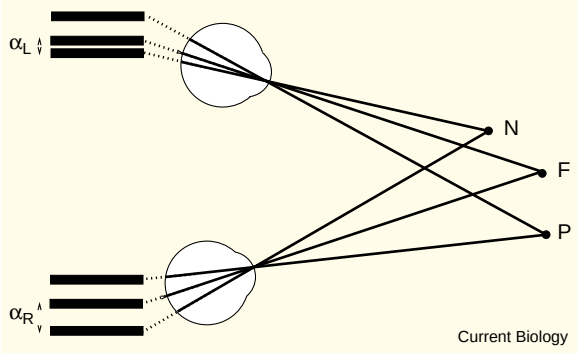

Figure 1. Geometry of stereopsis.

Both eyes are fixating point F, so the image of F falls on the fovea in both eyes. Point N lies closer to the observer than F, and as a result the images of N fall on different locations in the two eyes. The angular distance between the image of N and the fovea defines its position on the retina. The difference between these angles in the two eyes ($\alpha_L - \alpha_R$) defines the binocular disparity of point N. The activity of neurons should depend on this binocular disparity — they must be disparity-selective — if they are to make a useful contribution to stereopsis.

The emerging picture is that all parts of the visual cortex contain disparity-selective neurons, which suggests there is not an anatomical pathway specialized for the computations supporting stereopsis. Alternatively, this may only mean that simply demonstrating that a brain area contains disparity-selective neurons is not a reliable indicator of a role in stereopsis. A series of experiments from my own group (reviewed in [11]) has demonstrated that, at the earliest stages of cortical processing (area V1), the properties of disparity-selective neurons differ from the perceptual properties of stereopsis in several important ways. It is important to remember that binocular disparities may be used for several different functions — seeing depth, singleness of vision, control of binocular eye movements — and that simply measuring selectivity for disparity does not reveal what contribution (if any) a neuron makes to each of these.

More sophisticated neurophysiological tests of binocular function might help identify a cortical locus for stereopsis. Two such approaches have successfully demonstrated a close link between the activity of neurons in area V5/MT and stereopsis. First, electrical

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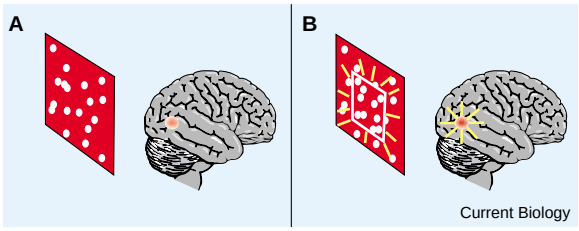

Figure 2.

One way in which the influence of attention on the fMRI response can give misleading results. Suppose some brain area was exclusively responsible for processing red stimuli (shown in red), and an experiment happened to use a red stimulus to explore stereopsis. The experiment compares responses to a plane (stimulus A) with those to a plane containing a feature defined by disparity (stimulus B). The appearance of this new feature in the scene will draw the subjects attention to the region of the disparity change (signified by the yellow lines). This shift in attention alone is sufficient to increase the fMRI signal recorded in parts of the brain that correspond to that spatial location. The influence of this change in attention may only be discernible in areas activated by the stimulus. In this very simple example, only one part of the brain is activated by either stimulus because of its color, but the fact that the response modulates with the changes in disparity might be taken (erroneously) as an indication that this area plays some role in disparity processing. Here, comparing responses to A and B identifies a brain area which is specialized for the attribute that is common to A and B, and fails to identify brain areas that are responsible for the attribute that is changing. Although it is naive to imagine that there is only one area of the brain activated by red stimuli, the principle of argument applies to any pair of stimuli where the shared attributes activate some brain areas more than others.

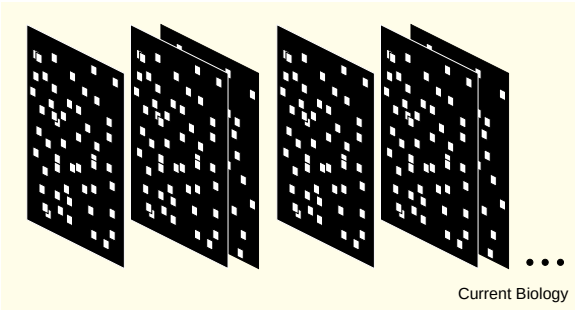

Figure 3.

Diagrammatic illustration of the stimulus used by Backus *et al.* [7]. A set of randomly located dots is used to define a planar surface (first image). This stimulus is alternated with a similar one in which two planar surfaces are transparently superimposed (the illustration shows the front surface as opaque to clarify the geometry, but in the stimulus actually used the dots comprising the back surface were visible through the front surface). Note that this change in disparity is not associated with any changes in the monocular stimuli, which always appear as homogeneous dot fields. Furthermore, even in the fused three-dimensional percept — the 'cyclopean' image — there are no new edges or shapes visible when the disparity changes. Thus there is no reason for the stimulus change to alter the location to which the the observers' attention is directed.

microstimulation in the vicinity of disparity-selective neurons in V5/MT influences animals' reports of depth [12]. Second, when viewing an ambiguous stimulus, changes in the perceived three-dimensional configuration (in the absence of any change in the external stimulus) are correlated with changes in neuronal activity [13,14]. These results suggest that area V5/MT is closely linked to stereopsis. But before concluding that part of stereo processing is localized there, it is important to conduct similar experiments for disparity-selective sites in other brain areas, especially in the ventral stream.

Taken together, the existing physiological data do not give a definitive answer to the central question posed above: is stereopsis localized to a distinct pathway within the brain? Furthermore, a great deal of new experimental work will be required to answer this question with traditional neurophysiological techniques. Faced with this prospect, it would be advantageous to employ a technique that allows the activity of many brain areas to be monitored simultaneously. This is the approach adopted by Backus *et al.* [7], who used functional magnetic resonance imaging (fMRI) in human subjects. This technique measures local changes in blood oxygenation within the brain, which in turn reflects some aspect of neural activity.

One of the chief limitations of fMRI arises from the fact that the activity measure is pooled over a certain volume of tissue, which contains many neurons. Suppose some hypothetical brain area was exclusively responsible for stereo depth sensation and contained a population of neurons that signalled whether objects were near or far. A near stimulus would activate all the near cells, but none of the far cells, while a far stimulus produces the opposite pattern of activity. An alternation in depth between near and far would then produce no change in the total number of spikes fired by the whole population of neurons. If the 'near' and 'far' neurons were not anatomically segregated, no modulation in the fMRI signal would result. (This argument assumes that the fMRI signal is determined by the total number of action potentials occurring in an area, but could be cast in terms of any other variable, if one was identified as more closely related to fMRI measures.)

An equally severe problem arises from the fact that the fMRI signal can be altered when the subject simply directs attention to a particular stimulus, without any change in the stimulus itself (see [15] for a review). This can generate quite misleading results (see Figure 2). Backus *et al.* [7] addressed some of these difficulties by completing a much more painstaking experiment than simply comparing activity to two stimuli. The basic design, like the great majority of fMRI experiments, exploited alternation of two stimuli — one uniform depth plane compared with two planes transparently superimposed (see Figure 3). Changes in blood oxygenation that follow the stimulus changes were then measured. By performing a parametric study of how the disparity between the planes affects both psychophysical performance and the fMRI signal, Backus *et al.* [7] have obtained compelling evidence

that there is a progression in the strength of stereo-related signals, with the strongest response in area V3A. For very small disparities, subjects were unable to detect any change at all. Once the disparity was large enough for subjects to detect, it also produced a significant fMRI modulation in V3A. Importantly, the size of the fMRI signal continued to grow with disparity, even for suprathreshold disparities. It is hard to see how these changes could be the result of extraneous factors like attention, which should be engaged by any suprathreshold stimulus.

As disparities became very large, subjects became unable to detect the presence of two distinct planes, and the fMRI signal declined back to baseline. Again, the changes in the fMRI signal were evident at disparities where the stimulus was still clearly visible, arguing against non-specific effects like attention. This close correlation with the psychophysical effects of disparity, combined with good controls for the effects of attention, make this a particularly strong fMRI result. Backus *et al.* [7] appear to have isolated a disparity mechanism that matches our stereoscopic perception. Interestingly, V3A is not considered a central component of the dorsal pathway (many illustrations have placed V3A in the ventral stream, see for example [16]). It may be that the pathway which elaborates stereo signals contains areas from both streams, and that the division of cortical visual processing into just two broad streams is too simple to accommodate all visual functions.

This is not the first fMRI study to use parametric comparisons with psychophysical data to permit strong conclusions about the role of cortical areas in human visual processing. But earlier studies of this type confirmed existing neurophysiological findings, exploring the relationship with contrast changes in V1 [17], and the strength of motion signals in human MT/MST [18]. The work of Backus *et al.* [7] is the first study to apply this powerful approach to reveal something that physiology has so far failed to do. The brain area identified here as particularly important in stereoscopic vision might never have become a candidate for neurophysiological experiments using disparity. On this occasion, human fMRI experiments can guide the investigations of other neurophysiologists, rather than the reverse.

References

1. Zeki, S. (1993). A Vision of the Brain. Blackwell Scientific, Oxford.
2. Zeki, S. (1978). Functional specialization in the visual cortex of rhesus monkey. Nature *274*, 423–428.
3. Albright, T.D. (1993). Cortical processing of visual motion. Rev. Oculomot. Res. *5*, 177–201.
4. Watanabe, M., Tanaka, H., Uka, T., and Fujita, I. (2001). Disparity-selective neurons in area V4 of macaque monkeys. J. Neurophysiol., in press.
5. Hinkle, D., and Connor, C. (2001). Disparity tuning in macaque area V4. NeuroReport *12*, 365–369.
6. Janssen, P., Vogels, R., and Orban, G.A. (1999). Macaque inferior temporal neurons are selective for disparity-defined three-dimensional shapes. Proc. Natl. Acad. Sci. U. S. A. *96*, 8217–8222.
7. Backus, B.T., Fleet, D.J., Parker, A.J., and Heeger, D.J. (2001). Human cortical activity correlates with stereoscopic depth perception. J. Neurophysiol. *86*, 2054–2068.
8. Ungeleider, L., and Mishkin, M. (1982). Two cortical visual systems. In Analysis of Visual Behavior, D. Ingle, M. Goodale, R. Mansfield, eds. (Cambridge, Mass: MIT Press), pp. 549–586.
9. Livingstone, M.S., and Hubel, D. H. (1987). Psychophysical evidence for separate channels for the perception of form, color, movement, and depth. J. Neurosci. *7*, 3416–3468.
10. Adams, D., Zeki, S. (2001). Functional organization of macaque V3 for stereoscopic depth. J. Neurophysiol. *86*, 2195–2203.
11. Cumming, B.G., and DeAngelis, G.C. (2001). The physiology of stereopsis. Annu. Rev. Neurosci. *24*, 203–238.
12. DeAngelis, G.C., Cumming, B.G., and Newsome, W.T. (1998). Cortical area MT and the perception of stereoscopic depth. Nature *394*, 677–680.
13. Dodd, J.V., Krug, K., Cumming, B.G., and Parker, A.J. (2001). Perceptually bistable three-dimensional figures evoke highchoice probabilities in cortical area MT. J. Neurosci. *21*, 4809–4821.
14. Bradley, D.C., Chang, G.C., and Andersen, R.A. (1998). Encoding of three-dimensional structure-from-motion by primate area MT neurons. Nature *392*, 714–717.
15. Kanwisher, N., and Wojciulik, E. (2000). Visual attention: insights from brain imaging. Nat. Rev. Neurosci. *1*, 91–100.
16. Van Essen, D.C., and DeYoe, E.A. (1994). Concurrent processing in the primate visual cortex. In The cognitive neurosciences, a handbook for the Field, M. Gazzaniga, ed. (Cambridge, USA: MIT Press), pp. 383–400.
17. Boynton, G.M., Engel, S.A., Glover, G.H., and Heeger, D.J. (1996). Linear systems analysis of functional magnetic resonance imaging in humas. J. Neurosci. *16*, 4207–4221.
18. Rees, G., Friston, K., and Koch, C. (2000). A direct quantitative relationship between the functional properties of human and macaque V5. Nat. Neurosci. *3*, 716–723.